KEY TO SPECIES OF MADAGASCAN *MACARANGA*

1. Mature leaves densely pubescent abaxially, peltate and/or caudate-acuminate.
  2. Leaves peltate.
    3. Leaf apex long-acuminate to caudate; floral bracts shallowly dentate .. *M. cuspidata* Baillon
    3'. Leaf apex acute, floral bracts fimbriate .... *M. ferruginea* Baker
  2'. Leaves not peltate .... *M. sphaerophylla* Baker

1'. Mature leaves glabrous or nearly so abaxially, neither peltate nor caudate.
  4. Blades with 1-3 pairs of laminar glands along the adaxial margin near the apex (and often scattered along the entire margin near the apex); apex obtuse or shortly and broadly acuminate .... *M. obovata* Baillon
  4'. Blades lacking paired laminar glands near apex (in *M. boutonioides* paired glands do sometimes appear, but the apex is acuminate).
    5. Leaves ovate and the margin convolute at the base, the basal laminar glands visible adaxially .... *M. boutonioides* Baillon
    5'. Leaves elliptic or obovate in most cases, if ovate then revolute or occasionally flat at the base.
      6. Material pistillate.
        7. Pistils and fruit bearing many (over 20) tentacle-like spines .... *M. macropoda* Baker
        7'. Pistils and fruit bearing few (up to 12) or no spines.
          8. Granules on lower leaf surface abundant (ca. one diameter apart); stems and/or petioles usually pubescent, occasionally glabrous.
            9. Fruiting pedicels 7-23 mm long, less than 0.5 mm wide .... *M. grallata* McPherson
            9'. Fruiting pedicels 2-10 mm long, over 0.5 mm wide .... *M. alnifolia* Baker
          8'. Granules on lower leaf surface relatively sparse (more than two diameters apart); stems and petioles glabrous.
            10. Leaves usually obtuse at apex and at base; petiole narrowly channeled; pistillate inflorescences rarely more than 5 cm .... *M. oblongifolia* Baillon
            10'. Leaves usually acute and acuminate at apex, attenuate to obtuse at base; petiole not or only shallowly channeled, often with a central ridge; pistillate inflorescences often more than 5 cm .... *M. ankafinensis* Baillon
      6'. Material staminate.
        11. Granules on lower leaf surface abundant (1-2 diameters apart) and clusters of buds 4-5 mm wide .... *M. alnifolia* Baker
        11'. Granules on lower leaf surface relatively sparse or clusters of buds 2 mm wide.
          12. Petiole not or only shallowly channeled, often with a central ridge.
            13. Petioles usually minutely puberulent, sometimes also bearing stiff, long hairs; granules on lower leaf surface abundant .... *M. grallata* McPherson
            13'. Petioles glabrous; granules on lower leaf surface sparse .... *M. ankafinensis* Baillon
          12'. Petiole narrowly channeled, without a central ridge.
            14. Leaf granules usually dark on drying; found above 700 m .... *M. macropoda* Baker
            14'. Leaf granules pale; found below 200 m .... *M. oblongifolia* Baillon

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Phylogenetic analysis and character evolution in Annonaceae

J.A. DOYLE & A. LE THOMAS

Summary: A phylogenetic analysis of Annonaceae based on morphological characters is presented, with tests of the relative strength of relationships among groups, justification and documentation of characters, and discussion of implications of the results for character evolution. The trees obtained show a high level of homoplasy and instability of relationships among groups, but rooting of the family and many major clades are relatively stable. The basal lines are *Anaxagorea* and the ambavioids, which have granular monosulcate pollen. Intermediate clades are the piptostigmoids, malmeoids (with columellar monosulcate pollen), and miliusoids (mostly with disulculate pollen). Taxa with inaperturate single pollen and tetrads — uvarioids (lianas), xylopioids, pseudosyncarps, and annonoids (including *Artabotrys*) — make up the inaperturate clade, which is linked with miliusoids by globose pollen and lamellar endosperm ruminations. Important trends in character evolution include: regularization of leaf venation (with several reversals), laminar stamens to stamens with prolonged to peltate to apiculate connective, sessile to capitate to elongate stigmas (with reversals to sessile), two origins of pseudosyncarpous and one of parasyncarpous fruits from apocarpous, thick to spiniform to lamelliform endosperm ruminations, and increases and decreases in chromosome number from n = 8. Petals are originally valvate and become imbricate in several lines. Wood characters, many aspects of floral and inflorescence morphology, and ovule number are especially homoplastic.

Résumé : Une analyse phylogénétique des Annonaceae, basée sur les caractères morphologiques, est présentée avec les tests de solidité relative des relations entre les groupes, l'apport de la documentation et de la justification des caractères et la discussion sur l'implication des résultats dans l'évolution des caractères. Les arbres obtenus montrent un fort degré d'homoplasie et d'instabilité des relations parmi les groupes; toutefois, l'enracinement de la famille et la plupart des clades majeurs sont relativement stables. *Anaxagorea* et les ambavioïdes, dont le pollen est monosulqué grenu, constituent les lignées basales. Les clades intermédiaires sont les piptostigmoïdes, les malmeoïdes (à pollen monosulqué columellaire), et les miliusoïdes (le plus souvent à pollen disulculé). Les taxa à pollen simple inaperturé ou en tétrades: uvarioïdes (lianes), xylopioïdes, pseudosyncarpes et annonoïdes (incluant *Artabotrys*) forment le clade des inaperturés lié aux miliusoïdes par le pollen arrondi et l'endosperme à ruminations lamelliformes. Plusieurs tendances importantes dans l'évolution des caractères sont mises en évidence: régularisation de la nervation foliaire (avec plusieurs réversions); étamines laminaires vers étamines à connectif prolongé, pelté, et apiculé; stigmates sessiles vers capités et allongés (parfois sessiles par réversion); deux origines des pseudosyncarpes et une origine des parasyncarpes à partir des apocarpes; ruminations de l'endosperme épaisses vers spiniformes et lamelliformes; augmentation et diminution du nombre chromosomique à partir de n = 8. La préfloraison des pétales est valvaire à l'origine et devient imbriquée dans plusieurs lignées. Les caractères du bois, plusieurs caractères de l'inflorescence et de la morphologie florale, ainsi que le nombre d'ovules sont particulièrement homoplasiques.

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INTRODUCTION

Annonaceae are the largest and morphologically most diverse family of primitive angiosperms ("Magnoliidae"), and because of their interest for angiosperm phylogeny and their important role in tropical forests (GENTRY 1993) they have attracted much systematic attention. Because of confusing variation and conflicts among traditionally emphasized floral characters, higher-level classification of the family has long been unstable, with little agreement on basal relationships and major intrafamilial groupings. Thus FRIES (1959) placed most members of the family (except the parasyncarpous African genera *Monodora* and *Isolona*, treated as a separate subfamily, and the aberrant neotropical genus *Tetrameranthus*, treated as its own tribe) into 14 groups and sorted these into the two tribes Uvariae and Unoneae, based on imbricate vs. valvate petal estivation, but he acknowledged exceptions to this distinction in both tribes. However, in the past 25 years comparative studies of new character sets have increased the data base of phylogenetically relevant information, and most recently cladistic methods have provided new insights into phylogeny and evolutionary scenarios.

Palynology was the first field to promise significant advances in understanding higher-level relationships in Annonaceae. In the first comprehensive pollen survey, WALKER (1971a, 1971b, 1972b), using light and scanning electron microscopy (LM, SEM), divided Annonaceae into three informal subfamilies and seven tribes. He argued that the most primitive group is the *Malmea* tribe of the *Malmea* subfamily, with columellar monosulcate pollen, and he recognized independent trends to tetrad pollen in his *Fusaea* and *Annona* subfamilies. Studies by LE THOMAS & LUGARDON (1974, 1976; LE THOMAS 1980/81), emphasizing African genera and using transmission electron microscopy (TEM) as well as LM and SEM, revealed that monosulcate taxa that WALKER (1971a) called "microtectate" have granular infratectal structure, and they considered these primitive based on comparison with other magnoliids and gymnosperms. HESSE et al. (1985), MORAWETZ & WAHA (1985), WAHA (1985, 1988), WAHA & HESSE (1988), and WAHA & MORAWETZ (1988) contributed important new data on exine structure of the granular monosulcate genus *Anaxagorea*, *Malmea* and related columellar monosulcates, and taxa with reduced exines, and extended the distribution of disulculate pollen.

Progressively more refined studies of other kinds of characters have revealed or confirmed many groupings at the intermediate level. For example, a survey of leaf anatomy in neotropical Annonaceae by VAN SETTEN & KOEK-NOORMAN (1986) greatly extended the earlier work of BEYER (1902). A study of seed anatomy by CHRISTMANN (1987) suggested the importance of the distribution of fibers and idioblasts (oil cells) in the seed coat. A comprehensive survey of fruit and seed characters led VAN SETTEN & KOEK-NOORMAN (1992) to classify most Annonaceae into 16 phenetic groups, plus *Polyalthia*, *Xylopia*, and several transitional and isolated genera. In a similar survey of floral morphology, VAN HEUSDEN (1992) recognized 19 groups and 12 isolated genera. Cytological studies (OKADA & UEDA 1984; MORAWETZ & WAHA 1985; MORAWETZ 1986a, 1986b, 1988; MORAWETZ & LE THOMAS 1988) have affected views on the basic chromosome number and yielded new characters and insights concerning nucleotypes.

The first cladistic analysis of Annonaceae (DOYLE & LE THOMAS 1994), which was intended especially to test ideas on pollen evolution, combined 11 pollen characters and 68 other macro- and micromorphological characters in a single data set, and used other Magnoliales as outgroups. In selecting taxa, we attempted to obtain a global sampling of major groups, while limiting our attention to taxa in which exine structure is known. This led to a certain bias in favor of African genera, which are best studied with TEM.

In general, this analysis (Fig. 1A) confirmed the ideas of WALKER (1971a) and LE THOMAS (1980/81) on pollen evolution. The Asian-American genus *Anaxagorea*, with granular monosulcate pollen and other magnolialian features, was basal (i.e., the sister group of other Annonaceae), followed by four small genera with similar pollen, the **ambavioids**, which formed either a clade or a paraphyletic series. Tetrads originated in two major lines: the **xylopioids** (part of WALKER's *Fusaea* subfamily), with granular structure; and the **annonoids** (WALKER's *Annona* subfamily), which become columellar. The xylopioids were linked with the **uvarioids**, which have granular inaperturate pollen; the annonoids with *Artabotrys*, which has columellar single grains with a reduced sulcus. The palynologically diverse genus *Polyalthia*, thought by LE THOMAS (1980/81) to mimic pollen trends in the family as a whole, was instead found to be polyphyletic, with members scattered among other taxa with similar pollen. Other important trends were a shift to columellar monosulcate pollen in the **malmeoids** (WALKER's *Malmea* tribe), multiple origins of di- or zonasulculate pollen, and independent origin of echinate sculpture in the *Monanthotaxis* group and *Pachypodanthium*. Many of the groups recognized by VAN SETTEN & KOEK-NOORMAN (1992) based on fruit and seed characters are also associated on these trees, but fewer of VAN HEUSDEN's (1992) groups based on floral characters.

In a paper on pollen ultrastructure of *Fusaea* and *Duguetia*, LE THOMAS et al. (1994) discussed the relationships of these and other pseudosyncarpous genera, which formed a clade within the uvarioids, and the characters that support them. Comparing the cladistic results with geographic distributions, LE THOMAS & DOYLE (in press) argued that the basal split into *Anaxagorea* (the only taxon with an Asian-American distribution) and the rest of the family (within which the basic lines are African and/or South American) reflects a mid-Cretaceous split into Laurasian and Northern Gondwanan lines, followed by Tertiary dispersal of some of the latter into Asia and Australia.

In a report devoted to the implications of palynology for relationships of African Annonaceae (DOYLE & LE THOMAS 1995), we modified our initial data set by adding two previously omitted African genera, *Afroguatteria* and *Mkilua*, and making slight changes in the data set based on more recent information. The most important change in the resulting trees (Fig. 1B) was that the annonoid and xylopioid tetrad groups and the inaperturate uvarioids all formed a single clade. This was a result of addition of *Afroguatteria*, which caused a shift of the echinate *Monanthotaxis* group away from the base of the xylopioid line and into the uvarioids, linked with *Uvaria* via *Afroguatteria*, so that tetrads were basic on the xylopioid line. The *Annona* group and the other annonoids with columellar tetrads formed a basal paraphyletic group relative to the xylopioids and uvarioids.